HOST SPECIFICITY IN ANOPLURA AND COEVOLUTION OF ANOPLURA AND MAMMALIA

ET

by H. W. Ludwig

1. — *What is host specificity?*

Host specificity is usually defined as the ability of a parasite species to thrive successfully and permanently on a single host species only. In this case we consider it to be a narrow host specificity and regard the parasite species as being stenohospitalic. In wide host specificity (that means in euryhospitalic parasites) a parasite species may live on two or more closely related hosts.

Host specificity is usually to be found in permanent and stationary parasites. The Anoplura are considered to have a rather high degree of host specificity, though there are many exceptions.

The above mentioned definition of host specificity is not sufficient as the following discussion may show. Host specificity is to be dealt with on different levels.

Instead of taking only parasite species and host species into consideration, we may also discuss host specificity on other (higher or lower) *taxonomic levels* (tab. 1).

Table 1. — Host-parasite relationships on different taxonomic levels.

Parasite taxon	Host taxon
Order Anoplura	Subclass Placentalia
Family Pedicinidae	Family Cercopithecidae
Genus *Pedicinus*	Family Cercopithecidae
Subgenus *Neopedicinus*	Subfamily Colobinae and Tribe Cercopithecini
Species *Pedicinus (Neopedicinus) pictus*	Genus *Colobus*
Subspecies *P. (N.) pictus gambiensis*	Subspecies *Colobus badius temminckii*

On all these levels there is clearly host specificity, and we should therefore not only ask the usual question : " Why is *Pedicinus pictus* restricted to genus *Colobus?* " but also, for instance : " Why are Pedicinidae restricted to Cercopithecidae ? "

We may further consider host specificity on microhabitat or *ecological level.*

In many cases a host species is parasitized by more than one louse species. The best known example for this is man, who harbors *Pthirus pubis* and two subspecies of *Pediculus humanus,* each of them mainly confined to a distinct region of the body. Another example is domestic cattle with three species of lice, *Linognathus vituli, Solenopotes capillatus* and *Haemotopinus eurysternus.* An extreme condition is shown by the South African Springbok, *Antidorcas marsupialis.* According to Weisser (1975) this host is infested by not less than six Anoplura species, five *Linognathus,* and one

Solenopotes. We may state generally, that the number of possible louse species on a host species is correlated to the number of different microbabitats or niches provided by tbe interactions between host and parasite. Therefore tbere seems to be usually (may be even always) an ecological separation on bost's surface : eacb louse species being adapted and restricted to its special and separate ecological nicbe. One of the louse species of *Antidorcas marsupialis, Linognathus digitalis,* seems to be absolutely restricted to tbe interdigital fossae of it's host — a most uncommon habitat for a sucking louse.

In most cases of multiple infestation (other examples are : *Hoplopleura* and *Polyplax* on Muridae, *Neohaematopinus* and *Enderleinellus* on Sciuridae) we know nothing about the ecological separation of the different louse species. We also do not know whether in the Springbok all possible louse species may live simultaneously on a single host individual. Finally, in most cases we do not know what happens when only one of the possible Anoplura species is present on a host individual : will it retain it's habitat range (as it is usually the case in human lice) (fig. 1 and 2c) or will it extend it's range occupying a bigger area (fig. 2b) or even tbe whole surface of host's body (fig. 2a) ?

Furtber research is urgently needed in the field of host specificity on ecological level. The main problems to be investigated are :

1. How is the distribution pattern on host's surface in cases of multiple infestation ?
2. What causes the niche specificity on tbe host ?
3. Why may the possible niche of a louse be reduced by competition with another louse species ?

There is finally a third point of view related to host specificity : host specificity on *geographic level.*

Normally a louse species infests it's bost species in the total range of the latter's geographic distribution (fig. 3a). Yet this is not always true. Besides the coincidence of louse and host distribution there may also be a partial occupancy only of host's range by tbe louse ; the hosts in the remaining part of the range may either be free of lice (fig. 3b) or infested by anotber louse species (fig. 3c). Here we have to ask whether the absence of a louse species in a part of it's host's distribution is directly caused by environmental factors, for instance temperature or humidity, or whether the environment acts indirectly by changing the habitat in the bost's fur.

II. — *What causes host specificity ?*

After having considered the different levels of host specificity we have now to ask for the factors causing host specificity in lice. Here again our knowledge is very scanty ; at least some of the factors I am going to mention are theoretical possibilities only — they may have or may not have a significance.

The *morphological factors* are rather obvious. A louse has to have tarsal claws that enable it to move in host's fur and to cling tightly to it. Especially the latter point is of vital importance for a louse, because the main technique of a host to get rid of it's lice is grooming by toes, teeth, tongue, and lips or scraping the body to other objetcs. *Haematopinus suis,* the hog louse, with claws adapted to the thick and widely spaced bairs of the pig will be completely helpless and unable to move and hold fast wben transferred to the dense and thin-haired fur of a mouse. In reverse the same is true when the mouse-infesting *Hoplopleura acanthopus* is transferred to a pig.

Large lice (e.g. *Haemotopinus, Pecaroecus, Pediculus*) have all legs and their tarsal claws of the same shape and size, all of them being able to grasp firmly to a single hair of host. This is not feasible in small Anoplura ; here the middle and hind legs only (most Hoplopleuridae and Polyplacidae) or even the hind legs only (Enderleinellidae) have a tibiotarsal complex that is big enough to seize host's hair. The other legs have small tarsal claws that are only able to hook to host's hair, thus facilitating movement.

Besides thickness of hairs also their structure and texture as well as density of fur and presence of different hair types may be of influence to host specificity.

Thickness of hairs is also significant in the process of egg deposition. During egg-laying the

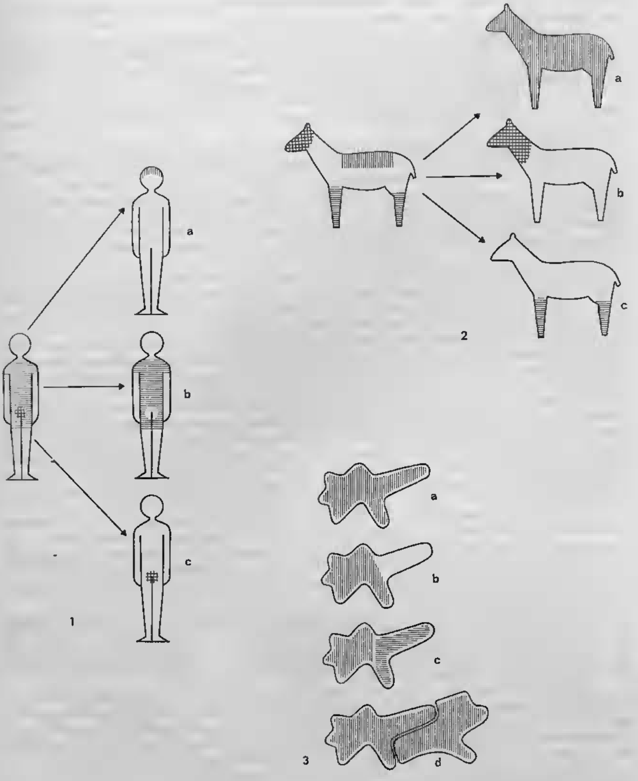

Fig. 1. — 1 : Ecological separation of human lice — a) *Pediculus humanus capitis*, b) *Pediculus humanus humanus* c) *Pthirus pubis*. 2 : Possibilities of ecological separation. 3 : Host specificity on geographic level.

female louse holds the hair to which the egg is to he glued between it's gonopods. Egg-laying is therefore impossihle, when the hair is either too thick or too thin.

When two congeneric louse species infest the same host, they sometimes differ markedly in head length, as several authors have ohserved. A longer head seems to be correlated with longer mouthparts. Thus, this may be considered adaptations to thickness and/or structure of host's skin which indicates the occupation of different microhabitats on host's surface.

Certainly tbere are more morphological adaptations, but we know nothing about, for instance, the significance of size, shape, density, and arrangement of setae, scales, and other surface structures in Anoplura.

As to *physiological factors* it was long ago assumed, that the incompatibility of strange, non-specific blood is the main or even exclusive factor causing host specificity, thus considering host specificity caused by monophagy. Meanwhile we know, that this is at least not always true. As early as 1948 Culpepper succeeded in rearing body lice permanently on rabbits. In 1968 Ludwig and Thiemes could rear the hog louse, *Haematopinus suis*, and the closely related louse of the wild boar, *Haematopinus apri*, without restriction on white laboratory mice. This of course does not mean that the lice were able to live on these substitute hosts — they only could thrive on their blood as sole source of food.

Although it is repeatedly and authentically reported, that human lice refuse to suck blood in certain individuals always or at least during a short period, we could never observe a refusal of non-specific blood nor even a refusal of other fluids including aqueous dye solutions and distilled water when feeding hungry lice through an artificial membrane (Häfner & Ludwig).

There is only one case reported, that lice die immediately after having taken strange blood : *Pediculus humanus* and *Haematopinus suis* will die inside 24 hours after being fed on guinea pigs. But they do not die of poisoning but of rupture of intestine due to crystallization of the blood. Therefore mortality is not caused by a chemical but by a physical factor.

On the other hand, there are marked differences in the suitahility of blood of different hosts to serve permanently as substitute food, as our experiments have shown (Ludwig 1973). The most remarkable result obtained in these experiments performed with *Pediculus humanus* and *Haematopinus suis* is the fact that suitability of blood is in no way correlated witb the systematic relationship of actual and substitute host. Besides this we know nothing about tbe biochemical or may be even immunological and serological properties of blood of different hosts, that affect it's ability to serve as food for a louse species. Here is a profitable field for future research !

Another factor certainly influencing host specificity is the microclimate (mainly temperature and humidity) in host's fur. As mentioned before, the microclimate may be directly influenced by the macroclimate of the surroundings, but surely it depends also on the activity of host's sweat glands and sebaceous glands, on host's metaholic rate, on the insulation by bluhber or fur, and on the temperature flow through host's surface. Even the specific smell of a host may he a necessary factor for a permanent thriving of a louse population.

Also *behavioral factors* seem to play an important rôle in host specificity. As mentioned above, a host has to develop efficient grooming techniques to keep it's louse population on a tolerable level. On the other hand, it is essential for a louse to avoid grooming by clinging tightly to the hairs, by quickly escaping out of a groomed area, or even by inhabiting those parts of host's surface only that cannot be reached hy grooming or scraping.

From all this it seems to be clear, that host specificity is never due to a single factor ; it is always caused by a multidimensional system of morphological, physiological and behavioral factors on both sides of the host-parasite system — each factor having it's counterpart in the other partner, thus a successful host-parasite relationship requires a very delicate equilibrium of many factors in botb partners. Both are to be exactly adapted to this mutual relationship.

Adaptedness of a louse is to be understood as the ability, to use host's resources and to avoid (at least in part) host's means of defense.

Adaptedness of a host is to be considered as the ability to stand the detrimental effects of louse infestation and to keep the louse population on an endurable level.

When we consider complete adaptedness as being ×, there are three possibilities, when a louse invades a new host :

	Adaptedness of louse population	Adaptedness of host population	Result
1.	×	×	lice establish on hosts
2.	< ×	⩽ ×	lice die
3.	⩽ ×	< ×	hosts die, lice die

III. — *What are the advantages aad the disadvantages of host specificity?*

At tbe very first sight bost specificity seems to be an obvious disadvantage to a parasite because it reduces drastically tbe number of potential host individuals. When the bost dies, its lice will die too very soon, unless tbey are able to reach a new host very quickly.

As lice are wingless and neither jumpers nor fast runners, they need very close contact to a new host for transler. In fact, besides the usually fatal interspecific contact between prey and predator, most contacts take part intraspecific between hosts ol the same species in common nests, in herds, or during copulation and tbe care of the young. Therefore in lice, as permanent and stationary parasites, absence of host specificity would mean only a very small diminution of the danger, to die together with the host. This diminution could, however, on no account cope with the obvious advantages gained by very exact mutual adaptations between lice and tbeir hosts, that make life easier lor botb partners of tbe system.

Looking backward over my remarks I am afraid that most ol what I have done was to state the scarcity of our knowledge and to ask many questions without answering them. But there are to be questions before tbere can be answers and I hope that some questions can be answered at this symposium or in the near future.

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List of Anoplura and hosts
(cf. Ludwig, 1968; Kim & Ludwig, 1978a).

Taxon (Family) (Genus)	Number of species		Hosts (Order) (Family)
Pediculidae	2		Primates
Pediculus		2	Hominidae, Cehidae, Pongidae
Pecaroecidae	1		Artiodactyla
Pecaroecus		1	Tayassuidae
Haematopinidae	22		Artiodactyla, Perissodactyla
Haematopinus		22	Bovidae, Suidae, Cervidae, Equidae
Microthoraciidae	4		Artiodactyla
Microthoracius		4	Camelidae
Echinophthiriidae	12		Pinnipedia, Carnivora
Echinophthirius		1	Phocidae
Antarctophthirus		6	Phocidae, Otariidae, Odohenidae
Latagophthirus		1	Mustelidae
Lepidophthirus		2	Phocidae
Proechinophthirus		2	Otariidae
Hybophthiridae	1		Tubulidentata
Hybophthirus		1	Orycteropodidae
Hamophthiriidae	1		Dermoptera
Hamophthirius		1	Cynocephalidae
Pthiridae	2		Primates
Pthirus		2	Hominidae, Pongidae
Pedicinidae	16		Primates
Pedicinus		16	Cercopithecidae
Polyplacidae	175		Rodentia, Lagomorpha, Insectivora, Primates
Polyplax		76	Muridae, Cricetidae, Rhizomyidae, Ahrocomidae, Sciuridae, Soricidae
Alenopthirus		1	Sciuridae
Ctenophthirus		1	Echimyidae
Docophthirus		1	Tupaiidae
Eulinognathus		23	Dipodidae, Pedetidae, Cricetidae, Ctenomyidae, Bathyergidae, Caviidae, Chinchillidae
Fahrenholzia		13	Heteromyidae
Haemodipsus		6	Leporidae
Lemurpediculus		2	Lemuridae
Lemurphthirus		3	Lorisidae
Neohaematopinus		41	Sciuridae, Cricetidae, Chrysochloridae
Phthirpediculus		2	Indriidae
Proenderleinellus		1	Muridae
Sathrax		1	Tupaiidae
Scipio		4	Thryonomyidae, Petromyidae
Neolinognathidae	2		Insectivora
Neolinognathus		2	Macroscelididae
Linognathidae	69		Artiodactyla, Carnivora, Hyracoidea
Linognathus		51	Bovidae, Giraffidae, Canidae
Solenopotes		10	Cervidae, Bovidae
Prolinognathus		8	Procaviidae
Ratemiidae	2		Perissodactya
Ratemia		2	Equidae
Hoplopleuridae	132		Rodentia, Insectivora, Lagomorpha
Hoplopleura		117	Muridae, Cricetidae, Sciuridae, Octodontidae, Echimyidae, Ochotonidae

Taxon (Family) (Genus)	Number of species		Hosts (Order) (Family)
Pterophthirus		5	Caviidae, Echimyidae
Ancistroplax		2	Soricidae
Haematopinoides		1	Talpidae
Schizophthirus		7	Gliridae, Zapodidae
Enderleinellidae	49		Rodentia
Enderleinellus		43	Sciuridae
Atopophthirus		1	Sciuridae
Microphthirus		1	Sciuridae
Phthirunculus		1	Sciuridae
Werneckia		3	Sciuridae

DISCUSSION

LLEWELLYN. — You referred to the crystallization of guinea-pig blood in the gut of a louse ; what is the nature of this crystallization ? Could it be precipitation of whole blood ?

LUDWIG. — It happens only with guinea-pig blood and might be crystallization of the haemoglobin.

LÉGER. — La « toxicité » du sang de cobaye pour *Haematopinus suis* est, en fait, une cristallisation de l'hémoglobine. Quelle en est la cause ? Ne serait-ce pas, par analogie avec ce qu'on observe chez les porteurs d'hémoglobine S, une cristallisation liée à une variation de la PO_2 ? Il serait intéressant de comparer les deux hémoglobines : S de l'homme et hémoglobine de cobaye.

AESCHLIMANN. — J'aimerais signaler que, chez les Tiques aussi, le sang de cobaye peut cristalliser dans l'intestin de l'Artbropode dans les jours qui suivent le repas.

BEAUCOURNU. — Lorsqu'il y a discordance entre l'aire de répartition de l'hôte et celle du pou, est-ce que le statut de l'hôte n'est pas à revoir ? Par exemple, *Hoplopleura edentula* Fahrenholz ne se rencontre, au moins en Italie, France et Espagne, que sur les *Clethrionomys glareolus* Schreber du groupe *nageri*. On peut se demander quel est le véritable statut de « *nogeri* ».

LUDWIG. — Yes. Perhaps.

WERTHEIM. — In table 1 you showed longevity of *H. suis* feeding on various hosts. What is the longevity of this louse on the natural host ?

LUDWIG. — The same as when feeding on mice.

CZAPLIŃSKI. — How can you explain the variation in longevity of *Haematopinus suis* males and females on different experimental hosts ?

LUDWIG. — In all cases (on all substitute hosts) females lived as long or longer than the males.

FAIN. — Peut-on obtenir des hybrides entre *Pediculus h. humanus* et *P. h. capitis* ? Que deviennent-ils.

LUDWIG. — Yes. The hybrids are found equally on the hair and clothing.

FAIN. — Peut-on élever *Pediculus humanus* sur des animaux ?

LUDWIG. — Yes, on rabbits.

EUZET. — A la suite de la communication de M. Ludwig et en reprenant ce que M. Maillard a souligné dans sa contribution, j'estime que l'on devra traiter de manière différente,

la spécificité c'est-à-dire les rapports d'une *espèce* parasite avec son ou ses hôtes

et les rapports qui se sont établis entre des unités systématiques de niveau supérieur (famille, ordre, classe) de parasites et d'hôtes.

Il faudrait proposer un autre terme pour ces rapports, car originellement la spécificité se concevait pour une espèce parasite.

OCCURRENCE OF ANOPLURA GENERA ON PLACENTALIA ORDERS

(Classification of Anoplura after Kim & Ludwig, 1978a)

Families and genera of Anoplura \ Orders of Placentalia	Artiodactyla	Perissodactyla	Sirenia	Hyracoidea	Proboscidea	Tubulidentata	Lagomorpha	Pinnipedia	Carnivora	Cetacea	Rodentia	Pholidota	Edentata	Primates	Dermoptera	Chiroptera	Insectivora	no. of species	
PEDICULIDAE																		2	
Pediculus														●					2
PERACOECIDAE																		1	
Peracoecus	●																		1
HAEMATOPINIDAE																		22	
Haematopinus	●	○																	22
MICROTHORACIIDAE																		4	
Microthoracius	●																		4
ECHINOPHTHIRIIDAE																		12	
Echinophthirius								●											1
Antarctophthirus								●											6
Latagophthirus									●										1
Lepidophthirus								●											2
Proechinophthirus								●											2
HYBOPHTHIRIDAE																		1	
Hybophthirus						●													1
HAMOPHTHIRIIDAE																		1	
Hamophthirius															●				1
PTHIRIDAE																		2	
Pthirus														●					2
PEDICINIDAE																		16	
Pedicinus														●					16
POLYPLACIDAE																		175	
Polyplax											●						○		76
Alenapthirus											●								1
Ctenophthirus											●								1
Docophthirus														●					1
Eulinognathus											●								23
Fahrenholzia											●								13
Haemodipsus							●												6
Lemurpediculus														●					2
Lemurphthirus														●					3
Neohaematopinus											●						○		41
Phthirpediculus														●					2
Proenderleinellus											●								1
Sathrax														●					1
Scipio											●								4
NEOLINOGNATHIDAE																		2	
Neolinognathus																	●		2
LINOGNATHIDAE																		69	
Linognathus	●								○										51
Solenopotes	●																		10
Prolinognathus				●															8
RATEMIIDAE																		2	
Ratemia		●																	2
HOPLOPLEURIDAE																		132	
Hoplopleura							○				●								117
Pterophthirus											●								5
Ancistroplax																	●		2
Haematopinoides																	●		1
Schizophthirus											●								7
ENDERLEINELLIDAE																		49	
Enderleinellus											●								43
Atopophthirus											●								1
Microphthirus											●								1
Phthirunculus											●								1
Wermeckia											●								3

● single or main occurence

○ additional occurence